

Trends in the maternal investment of harbour porpoises are uncoupled from the dynamics of their primary prey

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Harbour porpoises in the Bay of Fundy and Gulf of Maine feed primarily on Atlantic herring. Herring stocks have undergone dramatic fluctuations in abundance over the past three decades due to changes in fishing intensity. In order to understand the effects of these changes in prey abundance on the patterns of maternal investment, I examined interdecadal variation in the size of porpoise calves measured in August prior to weaning. Female harbour porpoises exhibited significant variation in maternal investment between 1970 and 1999. During the 1980s, females consumed more herring and produced larger calves. Surprisingly, however, this increased maternal investment occurred during the period of lowest prey abundance, perhaps because the herring stock assessment does not reflect the availability or quality of prey to female porpoises.

Keywords: harbour porpoises; herring; maternal investment; stock assessment

1. INTRODUCTION

Reproductive effort, that is the time and energy invested in producing offspring, is a central concept in life-history theory (Stearns 1992). In mammals, the energy invested in gestation and lactation is an important component of reproductive effort and pregnant and nursing females must increase their energy intake above the level required to meet their own metabolic requirements (Robbins 1983). The energy delivered to an offspring during gestation and lactation determines the size of the young at weaning, which may be an important determinant of juvenile survival and, thus, parental fitness (e.g. Clutton-Brock *et al.* 1982). Environmental variation may influence the strategies employed by female mammals for obtaining and transferring energy. When preferred food resources are scarce, females may increase their foraging effort or switch prey in order to meet the energetic costs of reproduction.

Marine mammals are large, long-lived and strongly iteroparous. Females in some species are known to vary their foraging effort related to reproductive investment in accordance with the availability of resources. For example, when prey is scarce, female Antarctic fur seals extend the duration of foraging trips and/or increase their foraging effort during trips (Costa *et al.* 1989; Boyd *et al.* 1994). Pinnipeds are particularly amenable to such studies because female seals and sea lions haul out at predictable times and places in order to give birth and nurse their pups. Furthermore, it is possible to estimate the energy invested by females in their offspring using isotopic techniques (Costa 1987) or by measuring the size of a pup at weaning (e.g. Georges & Guinet 2000).

Unlike pinnipeds, cetaceans live their entire lives in the water, often in environments that are inaccessible to researchers. In addition, many species are too large to capture, restrain and manipulate. Nevertheless, a few researchers have been able to provide some insight into maternal investment in cetaceans by taking advantage of unusual sampling opportunities. For example, Lockyer

(1986) examined fin whale carcasses at an Icelandic whaling station and demonstrated that body condition and ovulation rate were correlated with measures of prey abundance.

In this study, I examined variation in the maternal investment of one of the smallest cetaceans, the harbour porpoise *Phocoena phocoena*. Porpoises are tractable study animals because of their small size, highly synchronized reproductive schedule and the availability of a large series of samples from by-catches in commercial fisheries. In the Bay of Fundy and Gulf of Maine, where this study was conducted, each year mature females bear a single calf in May after a gestation of 11 months (Read 1990). The calf depends entirely on lipid-rich milk for the first three months after birth before it begins to forage in August or September (Smith & Read 1992; A. J. Read, unpublished data). Calves triple their body mass during this three-month period using energy derived solely from maternal sources. In this paper, I assume that the size of a calf in August is a reliable measure of maternal energy investment.

The diet of porpoises in the Bay of Fundy and Gulf of Maine is dominated by Atlantic herring (*Clupea harengus*), which comprises up to 80% of their total calorific intake (Smith & Gaskin 1974; Recchia & Read 1989; Gannon *et al.* 1998). Due to their small size, females are unable to store extensive energy supplies (Koopman 1998) and instead rely on supplementing their diet in order to obtain the extra energy required for their offspring. Female porpoises are thus considered to be 'income breeders' (Sibly & Calow 1986) and meet the costs of lactation by consuming a greater quantity of herring (Recchia & Read 1989) rather than drawing on stored reserves. Herring abundance in the Gulf of Maine has varied dramatically over the past few decades. Herring stocks were over-fished in the late 1960s, but have recovered recently to historically high levels under light fishing pressure (figure 1) (National Marine Fisheries Service 1998). In this paper, I describe the interdecadal variation in the maternal investment of harbour porpoises in the Bay of

Fundy and Gulf of Maine by examining changes in the size of calves measured in August, and relate this variation to changes in prey abundance.

2. METHODS

Porpoises were sampled in the Bay of Fundy in July, August and September 1970–1999. Most fieldwork was conducted near Grand Manan and Deer Island, New Brunswick, Canada. Collection methods varied over the three decades (table 1). In the 1970s, porpoises were hunted for research purposes by the late Professor D. E. Gaskin (e.g. Smith & Gaskin 1974). In the 1980s, many specimens were obtained from a commercial gill net fishery (Read & Gaskin 1988). Most of the porpoises from the 1990s were obtained as by-catches in herring weirs, which are large traps that are used to capture juvenile herring near the shore (Smith *et al.* 1983). Many of the porpoises obtained from the weirs were examined and released alive, particularly in the 1990s, but all other specimens were examined postmortem.

I considered a porpoise to be a calf in a postmortem examination if it exhibited an incomplete first growth layer group in its dentine ($n=31$) or if milk was present in its fore-stomach ($n=1$). I identified live porpoises as calves if their teeth were not fully erupted ($n=10$) or if they were observed closely associated with a lactating female prior to capture ($n=9$). Four solitary and emaciated calves from herring weirs (one in the 1980s and three in the 1990s) were excluded from the analysis because they had been separated from their mothers for some time prior to measurement.

I used the size of calves in August as a measure of total maternal investment. I examined variation in the standard length and body mass of calves over the three decades, but both measurements were not available from all individuals. I estimated mass in 18 cases using equations that incorporated length and girth as predictive variables (e.g. Read & Tolley 1997). Additional data were collected during necropsies of lactating females including (i) blubber thickness, which was measured laterally at the level of the dorsal fin (Koopman 1998), (ii) the proportion of individuals possessing a corpus luteum, indicating recent ovulation or pregnancy (Read 1990), and (iii) the numerical proportion of herring in the fore-stomach (Gannon *et al.* 1998). I excluded lactating females killed in herring weirs from the dietary analysis because these individuals had probably been feeding on herring just prior to death.

I derived annual estimates of herring biomass from a virtual population analysis (VPA) that was used in the most recent assessment of herring stocks (National Marine Fisheries Service 1998). Harbour porpoises feed primarily on juvenile herring (Smith & Gaskin 1974; Recchia & Read 1989; Gannon *et al.* 1998) so I examined trends in the biomass of fish in age classes 2–4 years. In order to obtain annual estimates of biomass, I multiplied the number of fish in each age class by the mean weight of that class and then summed the three age classes for each calendar year. Annual estimates of the biomass of juvenile herring derived in this manner were available from 1970 to 1997.

I grouped data on prey abundance and calf size by decade (1970–1979, 1980–1989 and 1990–1999) and used analysis of variance for examining temporal differences in the size of porpoise calves and the Bonferroni method for comparing means. In cases where variances were heterogeneous, I used the Tamhane test, which is a conservative pairwise comparison, for comparing means. I conducted all analyses using SPSS version 9.0.

Table 1. *Sample sizes of harbour porpoises from the Bay of Fundy, Canada, during 1970–1999*

(The numbers of calves examined in August are indicated in parentheses.)

decade	hunted	gill net	herring weir	stranded	total
1970s	100 (12)	0 (0)	43 (1)	0 (0)	143 (13)
1980s	2 (0)	316 (18)	31 (2)	0 (0)	349 (20)
1990s	0 (0)	104 (3)	318 (14)	17 (1)	439 (18)

3. RESULTS

The mean annual biomass of juvenile herring in the Gulf of Maine (\pm s.d.) decreased from $296\,000 \pm 190\,000$ metric tonnes (mt) in the 1970s to $178\,000 \pm 70\,000$ mt in the 1980s and then increased dramatically to $1\,003\,000 \pm 702\,000$ mt in the 1990s (figure 1). Thus, herring abundance increased almost sixfold between the 1980s and 1990s.

The masses ($F=15.2$, d.f.=2,42 and $p<0.01$) and lengths ($F=14.7$, d.f.=2,48 and $p<0.01$) of calves in August varied significantly over the three decades (table 2). All pairwise comparisons of calf size between decades were significant ($p<0.05$) with the exception of body mass between 1970 and 1990 ($p=0.16$). Unexpectedly, however, the changes in calf size did not reflect the trends in the abundance of herring. In particular, calves were largest in the 1980s when prey abundance was lowest (table 2). Paradoxically, as prey abundance decreased 40% from the 1970s to the 1980s, the mass of calves increased by more than 50%.

In order to examine whether the capture method biased estimates of calf size, I compared the size of calves obtained from herring weirs over the three decades. I included calves from July ($n=5$) and September ($n=5$) in order to increase the sample size. Too few observations of mass were available to allow comparison between decades, but the mean lengths of calves sampled from the weirs ($F=4.13$, d.f.=2,24 and $p=0.03$) reflected those of the overall sample (table 2). Despite the small sample, the mean length of calves from the weirs in the 1980s was significantly greater than the corresponding mean length in the 1970s ($p=0.02$). Thus, the method of sample collection was not responsible for the observed variation in calf size. In addition, there were no significant differences ($p>0.05$) between the mean lengths of male and female calves in any decade, nor in the mean dates of sample collection in August between the three decades. Finally, there was no indication from the growth of foetuses or the size or development of corpora lutea that the timing of ovulation, conception or parturition varied over the study period. Thus, calves examined in August would have been of the same developmental stage in each decade.

Maternal size and condition did not vary over the three decades. There were no significant differences in the lengths ($F=2.23$, d.f.=2,34 and $p=0.12$), masses ($F=0.47$, d.f.=1,22 and $p=0.50$) or blubber thicknesses ($F=1.71$, d.f.=1,18 and $p=0.21$) of lactating females measured in August between decades, although observations of mass and blubber thickness were not

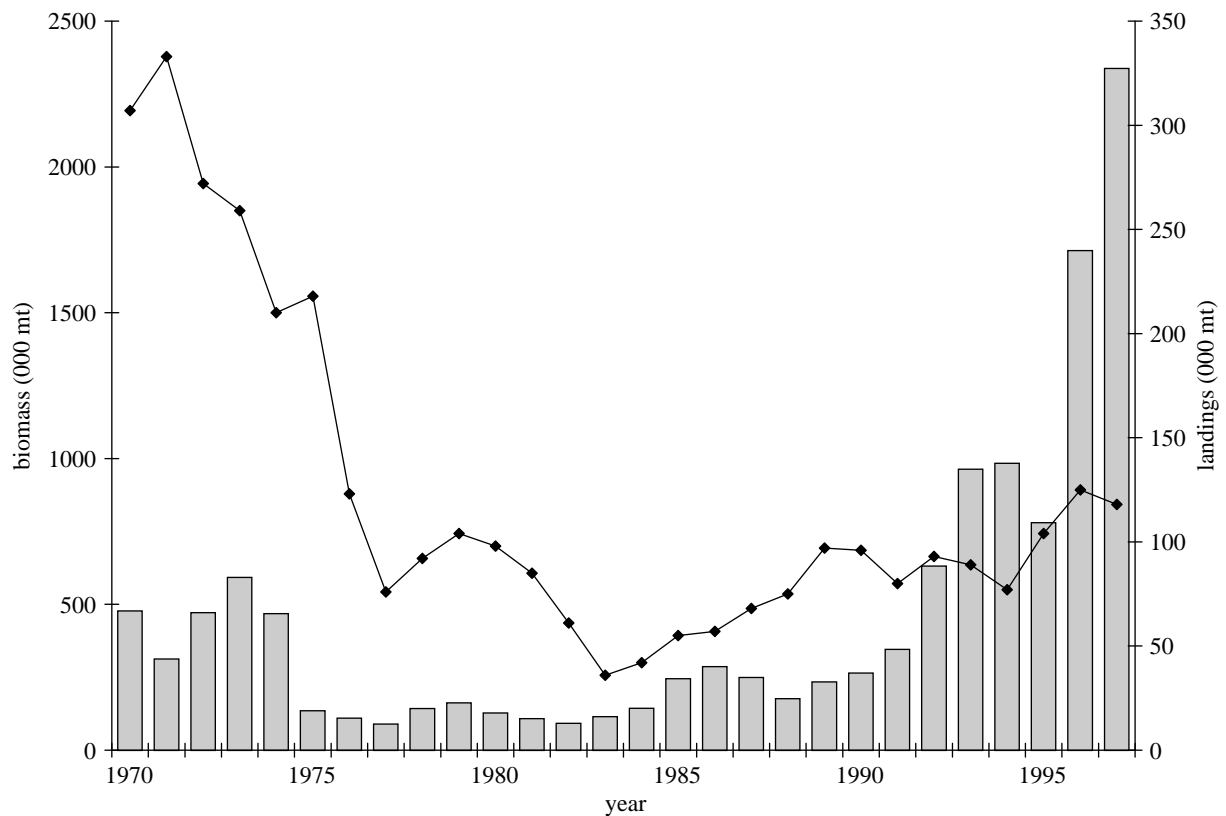


Figure 1. Temporal variation in the biomass of juvenile (ages 2–4 years) Atlantic herring (*C. harengus*) from the Gulf of Maine in 1970–1999 (bars). Commercial fisheries' landings of all age classes are shown for the same time-period (line). Data from US National Marine Fisheries Service (1998).

available from the 1970s (table 3). All lactating females examined in August possessed a corpus luteum, indicating recent ovulation. The proportion of herring in the diet of lactating females from July to September was greatest in the 1980s and least in the 1970s (table 3), reflecting the interdecadal variation in calf size. Thus, females produced the largest calves when their diet contained the greatest proportion of herring, although this occurred when herring was least abundant.

4. DISCUSSION

The maternal investment of harbour porpoises in the Bay of Fundy, as measured by the size of their calves in August, varied significantly between 1970 and 1999. In the 1980s, lactating females consumed a greater proportion of herring and produced larger calves than during the other two decades. Surprisingly, however, this increase occurred during a period of depressed prey abundance following the crash of herring stocks in the Gulf of Maine. This variation in maternal investment was not the result of biases due to the method of capture, differences in the sex ratio or changes in reproductive timing.

Several factors could explain the apparent incongruency between the patterns of maternal investment and the dynamics of the prey. First, it is conceivable that the estimates of prey biomass derived from the VPA were inaccurate and that the true trajectory of herring biomass in the Gulf of Maine was fundamentally different from that shown in figure 1. There is some uncertainty regarding

Table 2. Decadal variation in the size of harbour porpoise calves from the Bay of Fundy

(Means are presented with their associated standard deviations and sample sizes are given in parentheses.)

decade	mass by all methods in August (kg)	length by all methods in August (cm)	length by weir only in July–September (cm)
1970s	17 ± 5.2 (10)	93 ± 8.2 (13)	92 ± 5.2 (4)
1980s	25 ± 2.9 (19)	106 ± 5.7 (20)	104 ± 4.3 (4)
1990s	21 ± 4.7 (16)	100 ± 7.4 (18)	99 ± 6.9 (19)

estimates of biomass in the late 1990s because the most recent herring age classes have been represented for only a few years in the catch record (National Marine Fisheries Service 1998). Nevertheless, the general trends of this stock complex are well supported by fishery-independent data, including trawl survey catches (National Marine Fisheries Service 1998) and indices of larval abundance (Smith & Morse 1993). With this supporting evidence, it seems unlikely that the VPA is fundamentally biased.

Second, the VPA included several spawning stocks of Atlantic herring in the Gulf of Maine and it is likely that these stock components had experienced independent changes in biomass over the previous three decades (National Marine Fisheries Service 1998). It is therefore possible that one spawning stock of herring was

Table 3. *Decadal variation in the size, condition and diet of lactating female harbour porpoises from the Bay of Fundy*

(The figures presented are data on diet from females examined between July and September excluding specimens from weirs. All other data were taken from females obtained from all capture methods and examined in August. Means are presented with their associated standard deviations and sample sizes are given in parentheses.)

decade	length (cm)	mass (kg)	blubber thickness (cm)	ovulation rate	proportion of diet herring
1970s	160 ± 5.7 (8)	—	—	1.0 (8)	0.28 (8)
1980s	154 ± 5.6 (15)	61 ± 5.2 (15)	1.8 ± 0.3 (15)	1.0 (15)	0.65 (28)
1990s	156 ± 7.4 (14)	59 ± 7.7 (9)	1.6 ± 0.4 (5)	1.0 (6)	0.49 (8)

particularly important to female porpoises and that this stock experienced changes in abundance that are not reflected in figure 1. For example, the trajectory of biomass in the coastal stock of herring was slightly different from that of the stock on Georges Bank (National Marine Fisheries Service 1998). However, we know from satellite telemetry studies that individual porpoises move throughout the Bay of Fundy and Gulf of Maine, sampling most herring spawning aggregations (Read & Westgate 1997). In addition, calf size in August reflects the energetic investment of female porpoises over the entire year (11 months of gestation followed by three months of lactation). Thus, it is likely that female porpoises integrate local variation in prey abundance over the course of their reproductive cycle.

Third, it is possible that the variation in maternal investment reflects changes in porpoise density as well as changes in prey abundance. Many thousands of harbour porpoises were killed in gill net fisheries during the study period, particularly in the 1980s and early 1990s (e.g. Bisack 1997). No time-series of abundance estimates are available for 1970–1999, but it is likely that the density of porpoises was reduced by these by-catches over this period, potentially increasing the per capita availability of prey. I consider this explanation unlikely in accounting for the observed variation in maternal investment because the changes in porpoise density were probably small compared with the massive variation in prey abundance. It is conceivable, for example, that porpoise density declined by half between 1970 and 1999, but during this period the biomass of juvenile herring varied more than an order of magnitude. In addition, the trends in maternal investment are not consistent with the predictions of this hypothesis. Calf size decreased between the 1980s and 1990s even as porpoise by-catches continued and, presumably, porpoise density continued to decline.

If the factors described above do not explain the apparent incongruence between the patterns of maternal investment and prey dynamics, what is responsible for this unexpected result? I believe the trends in herring abundance generated from the VPA do not necessarily reflect the availability or quality of prey to female porpoises. It is possible, for example, that female porpoises were able to forage more profitably during periods of low prey abundance. Atlantic herring form dense schools, largely as an anti-predator strategy (Cushing & Harden Jones 1968). We do not know how school size or composition varied with abundance in the

Gulf of Maine, but it is possible that female porpoises were able to increase their foraging success in periods of low prey abundance by focusing their efforts on small, dispersed schools. More information on the foraging behaviour of harbour porpoises is required in order to test this hypothesis.

It is also possible that, as the density of herring decreased in the Gulf of Maine, the size and quality of individual prey improved. In order to address this hypothesis, I examined changes in the size of juvenile herring over the three decades. There were no decadal differences in the masses of two-year-old herring, but the masses of three- and four-year-old fishes were significantly lower in the 1990s than in the other two decades ($p < 0.01$). Thus, although the total biomass of juvenile herring increased between the 1980s and 1990s, the size of individual fishes decreased. If female porpoises maintained a constant predation rate (e.g. number of prey consumed per day) their energetic intake would have declined in the 1990s because of the decrease in the average size of their prey. In addition, the energy content of individual fishes may also have shown a density-dependent decrease between these decades. The lipid content of herring in this area is known to exhibit inter-annual variation (Stoddard 1968), although there are no data on the energy content of herring for complementing the analysis of changes in prey size. The effect of a decrease in fat content would be most keenly felt during lactation when female porpoises nurse their calves with lipid-rich milk.

These results confirm the suggestion that offspring size is a plastic life-history parameter in this species (Read & Gaskin 1990), although the ultimate effects of this variation on juvenile survival and maternal fitness are not yet known. The present observations also indicate that the dynamics between porpoise and their primary prey are complex and that density-dependent changes in herring stocks may have important consequences for their predators. The apparent uncoupling of maternal investment and prey dynamics in this species serves as a cautionary note for researchers using commercial fisheries' assessments for studying the ecology of marine mammal predators and underscores the need for measuring prey abundance, availability and quality on relevant scales.

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REFERENCES

- Bisack, K. D. 1997 Harbor porpoise bycatch estimates in the U.S. New England multispecies sink gillnet fishery: 1994 and 1995. *Rep. Int. Whal. Comm.* **47**, 699–703.
- Boyd, I. L., Arnould, J. P. Y., Barton, T. & Croxall, J. P. 1994 Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *J. Anim. Ecol.* **63**, 703–713.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. 1982 *Red deer. Behavior and ecology of two sexes*. University of Chicago Press.
- Costa, D. P. 1987 Isotopic methods for quantifying material and energy intake of free-ranging marine mammals. In *Approaches to marine mammal energetics* (ed. A. C. Huntley, D. P. Costa, G. A. J. Worthy & M. A. Castellini), pp. 43–66. Lawrence, KS: Society for Marine Mammalogy.
- Costa, D. P., Croxall, J. P. & Duck, C. D. 1989 Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology* **70**, 596–606.
- Cushing, D. H. & Harden Jones, F. R. 1968 Why do fish school? *Nature* **218**, 918–920.
- Gannon, D. P., Craddock, J. E. & Read, A. J. 1998 Autumn diet of harbor porpoises (*Phocoena phocoena*) in the Gulf of Maine. *Fish. Bull. US* **96**, 428–437.
- Georges, J.-Y. & Guinet, C. 2000 Maternal care in the Subantarctic fur seals on Amsterdam Island. *Ecology* **81**, 295–308.
- Koopman, H. N. 1998 Topographical distribution of the blubber of harbor porpoises (*Phocoena phocoena*). *J. Mamm.* **79**, 260–270.
- Lockyer, C. 1986 Body fat condition in northeast Atlantic fin whales, *Balaenoptera physalus*, and its relationship with reproduction and food resource. *Can. J. Fish. Aquat. Sci.* **43**, 142–147.
- National Marine Fisheries Service 1998 *Report of the 27th Northeast Regional Stock Assessment Workshop*. Woods Hole, MA: Northeast Fisheries Science Center.
- Read, A. J. 1990 Reproductive seasonality of harbour porpoises from the Bay of Fundy. *Can. J. Zool.* **68**, 284–288.
- Read, A. J. & Gaskin, D. E. 1988 Incidental catch of harbor porpoises by gill nets. *J. Wildl. Mgmt* **52**, 517–523.
- Read, A. J. & Gaskin, D. E. 1990 Changes in growth and reproduction of harbour porpoises *Phocoena phocoena* from the Bay of Fundy. *Can. J. Fish. Aquat. Sci.* **47**, 2158–2163.
- Read, A. J. & Tolley, K. A. 1997 Postnatal growth and allometry of harbour porpoises from the Bay of Fundy. *Can. J. Zool.* **75**, 122–130.
- Read, A. J. & Westgate, A. J. 1997 Monitoring the movements of harbour porpoises (*Phocoena phocoena*) with satellite telemetry. *Mar. Biol.* **130**, 315–322.
- Recchia, C. R. & Read, A. J. 1989 Stomach contents of harbour porpoises, *Phocoena phocoena*, from the Bay of Fundy. *Can. J. Zool.* **67**, 2140–2146.
- Robbins, C. T. 1983 *Wildlife feeding and nutrition*. New York: Academic Press.
- Sibly, R. M. & Calow, P. 1986 *Physiological ecology of animals*. Oxford, UK: Blackwell Scientific Publications.
- Smith, G. J. D. & Gaskin, D. E. 1974 The diet of harbor porpoises (*Phocoena phocoena* (L.)) in coastal waters of eastern Canada, with special reference to the Bay of Fundy. *Can. J. Zool.* **52**, 777–782.
- Smith, G. J. D., Read, A. J. & Gaskin, D. E. 1983 Incidental catch of harbor porpoise, *Phocoena phocoena* (L.), in herring weirs in Charlotte County, New Brunswick, Canada. *Fish. Bull. US* **81**, 660–662.
- Smith, R. J. & Read, A. J. 1992 Consumption of euphausiids by harbour porpoise (*Phocoena phocoena*) calves in the Bay of Fundy. *Can. J. Zool.* **70**, 1629–1632.
- Smith, W. G. & Morse, W. W. 1993 Larval distribution patterns: early signals for the collapse/recovery of Atlantic herring *Clupea harengus* in the Georges Bank area. *Fish. Bull. US* **91**, 338–347.
- Stearns, S. C. 1992 *The evolution of life histories*. Oxford University Press.
- Stoddard, J. H. 1968 Fat contents of Canadian Atlantic herring. *Fish. Res. Bd Can. Tech. Rep.* **79**, 1–23.

